
SCENT OF DISINTERRED SOIL AS AN OLFACTORY CUE USED BY RACCOONS TO LOCATE NESTS OF DIAMOND-BACKED TERRAPINS (*MALACLEMYS TERRAPIN*)

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Abstract.—We studied predation of nests of Diamond-backed Terrapin (*Malaclemys terrapin*) in North Inlet, South Carolina, USA, by documenting nest predators and by determining the sensory cues used by Raccoons (*Procyon lotor*) to locate terrapin nests. We used visual surveys and camera traps to monitor nesting sites and identify the local nest predator community. We conducted a series of experiments to determine whether Raccoons use visual or olfactory cues to identify terrapin nests. We also determined which olfactory cues were important to Raccoons foraging for terrapin eggs. Several potential nest predators were identified at terrapin nesting sites; however, Raccoons were the predominant nest predators throughout the study area. We constructed simulated nests to determine which scent cues Raccoons used to locate terrapin nests. Scent from disinterred soil resulted in nearly four-times higher predation rates compared to terrapin-scented simulated nests. Visual markers did not affect predation rates. Results indicate that scent associated with disinterred soil is the primary olfactory cue used by Raccoons to identify locations of terrapin nests.

Key Words.—camera trap; eggs; predation; salt marsh; scent; simulated nest; turtle

INTRODUCTION

Terrestrial nest predators are a major source of mortality for aquatic turtles (Iverson 1991). High predation rates on turtle nests can result in poor juvenile recruitment and therefore negatively affect demographic structure of local populations (Congdon et al. 1993, 1994; Feinberg and Burke 2003; Browne and Hecnar 2007). Diamond-backed Terrapins (*Malaclemys terrapin*) are estuarine specialists endemic to coastal salt marshes of the eastern, southeastern, and Gulf coasts of the United States (Ernst et al. 1994). Terrapins are a species of concern over most of their geographic range due to habitat loss and mortality caused by crab pots, commercial harvest, and nest predation by terrestrial vertebrate predators (Seigel and Gibbons 1995; Roosenburg et al. 1997; Butler et al. 2006). For example, in some Diamond-backed Terrapin populations, predation rates of nests exceeds 90% (Feinberg and Burke 2003; Butler et al. 2004).

Raccoons (*Procyon lotor*) are common predators on terrapin eggs over much of the geographic range of terrapins (Burger 1977; Roosenburg and Place 1994; Feinberg and Burke 2003; Butler et al. 2004). Raccoons exploit anthropogenically altered habitats and consequently, increases in Raccoon populations are often associated with human development (Prange and Gehrt 2004). Because of widespread development in coastal areas, terrapin nesting habitats, even in conser-

vation easements, are often located near human habitation where increased Raccoon population density may result in elevated predation (Feinberg and Burke 2003; Munscher et al. 2012). Terrapin nests may be particularly susceptible to predation because suitable nesting sites are often restricted in estuarine environments due to limited availability of open, sandy areas that are free from tidal inundation (Roosenburg 1994). Accordingly, nest density can be relatively high in suitable habitats (e.g., up to 0.269 nests/m², Feinberg and Burke 2003; 0.123 depredated nests/m², this study). Limited nesting areas and high nest density combined with relatively large numbers of resident Raccoons likely increases predation on terrapin eggs (Roosenburg and Place 1994; Munscher et al. 2012). Moreover, removal or absence of Raccoons results in higher nest survival (Munscher et al. 2012; Roosenburg et al. 2014).

Raccoons are highly effective predators possessing good vision, exceptional tactile perception, and an excellent sense of smell (Zelveloff 2002). Accordingly, Raccoons may use a variety of sensory modalities, alone or in combination to identify turtle nests, including those of Diamond-backed Terrapins. For example, Raccoons apparently use vision to locate nests of some turtle species such as the Alligator Snapping Turtle (*Macrochelys temminckii*; Holcomb and Carr 2013). Unlike terrapins, Alligator Snapping Turtles construct visually conspicuous nests characterized by rounded piles of soil (Woolsey 2005; Holcomb and Carr 2013). In contrast, nesting ter-

rapins attempt to hide the location of nests by obliterating evidence of digging and disguising nests by spreading sand and surface debris over the nest (Burger 1977). Moreover, experiments conducted on terrapins and other emydid turtles demonstrated that flagging nests with visual markers did not affect predation rates, suggesting visual cues were not used by Raccoons searching for terrapin nests (Tuberville and Burke 1994; Burke et al. 2005; Strickland et al. 2010). Tactile perception is a critical component of Raccoon foraging behavior with nearly two-thirds of their somatosensory cortex dedicated to processing tactile information received from their forepaws (Welker and Seidenstein 1959; Welker et al. 1964). Tactile searching, however, would likely not be an efficient primary method for locating small (roughly 6 cm diameter) nest openings dispersed throughout hundreds of square meters of nesting habitat (Burger 1977; Feinberg and Burke 2003; Munscher et al. 2012). Finally, several studies on both ground nesting birds and turtles indicate that Raccoons rely heavily on olfaction to locate nests with eggs (Wilhoft et al. 1979; Congdon et al. 1983; Whelan et al. 1994; Butler et al. 2004; Burke et al. 2005). Unlike tactile and visual sensory modalities, olfaction would be an effective way for Raccoons to search broad areas for terrapin nests. Collectively, these observations suggest that scent is the primary cue used by Raccoons to locate terrapin nests.

Olfactory-searching predators foraging for turtle eggs must be able to follow discontinuous scent plumes to specific point sources (i.e., nests) scattered throughout the environment (Ache and Young 2005). While numerous studies have suggested possible scent cues used by Raccoons to locate turtle nests, few have experimentally tested which specific olfactory cue or cues are used to identify and locate terrapin nests. For example, Raccoons potentially could identify nest locations by scent of the nesting female, eggs themselves, or both (Congdon et al. 1983; Spencer 2002; Burke et al. 2005). Burke et al. (2005) suggested that in addition to scent of nesting females, soil surface disturbance and/or salt water may provide cues for predators to indicate presence of nests. While studying Painted Turtle (*Chrysemys picta*) nest predation, Strickland et al. (2010) also noted increased predation associated with surface soil disturbances. The experimental designs used by Burke et al. (2005) and Strickland et al. (2010), however, did not allow them to determine whether increased nest predation rates were due to visual or olfactory stimuli.

In addition to Raccoons, several other animal species (e.g., ants, birds, armadillos, snakes, mice, and foxes) are predators on Diamond-backed Terrapin eggs (Burger 1977; Zimmerman 1992; Butler et al. 2004; Roosenburg et al. 2014). The impact of these nest predators likely varies across the broad geographic range of the terrapin (Burger 1977). For example, Nine-banded Armadillos

(*Dasypus novemcinctus*) are predators on Diamond-backed Terrapin nests in Florida (Butler et al. 2004); whereas ants caused terrapin egg mortality in New Jersey (Burger 1977), and Eastern Kingsnakes (*Lampropeltis getula*) depredated nests in Maryland (Roosenburg et al. 2014). To our knowledge no prior studies have documented the suite of Diamond-backed Terrapin nest predators in South Carolina.

The purpose of this study was twofold: our first objective was to document types of terrapin nest predators in North Inlet, South Carolina, USA. Our second objective was to determine the sensory cues used by Raccoons to locate terrapin nests. To accomplish these goals, we monitored terrapin nesting activity throughout the spring and summer nesting season and identified terrapin nest predators using camera traps, visual site surveys, and trackboard surveys. To determine which sensory cues are used by Raccoons to identify terrapin nests, we conducted a series of experiments using simulated nests. The first experiment tested the hypothesis that Raccoons identify nest locations using scent left by the female during the process of nest construction. This initial experiment was followed by two additional experiments to isolate specific sensory cues used by Raccoons to locate terrapin nests.

MATERIALS AND METHODS

Study area.—The study was conducted at Winyah Bay National Estuarine Research Reserve, managed by the Belle Baruch Research Institute, Georgetown County, South Carolina (33.35°N, 79.20°W; Fig. 1). The site consists of approximately 7,082 ha of Lowland Forests and Salt Marsh habitat including extensive *Spartina* spp. (cordgrass) flats, tidal creeks, and barrier islands.

Site selection and descriptions.—We conducted extensive site surveys within the study area and identified shared landscape characteristics associated with typical Diamond-backed Terrapin nesting sites. National Wetlands Inventory (NWI) land-use and orthorectified aerial photographs were compiled in ArcGIS and ArcView (version 10.3.1, Esri, Inc., Redlands, California) following available digital data predicted to be associated with terrapin nesting (Cowardin et al. 1979). Based on this analysis, terrapin nesting sites in North Inlet are characterized by: (1) fine-grained sand; (2) NWI class E2EM1 habitat (estuarine, intertidal, emergent wetlands); (3) salt marsh flora (e.g., *Spartina patens* and *Juncus roemerianus*); and (4) proximate surface water (i.e., located within 100 m of nest sites). Using these criteria, we identified 13 potential nesting sites. From these, we chose three sites to include in our study based on the following constraints: (1) direct evidence of nesting; (2) site independence (i.e., > 200 m apart); and (3)

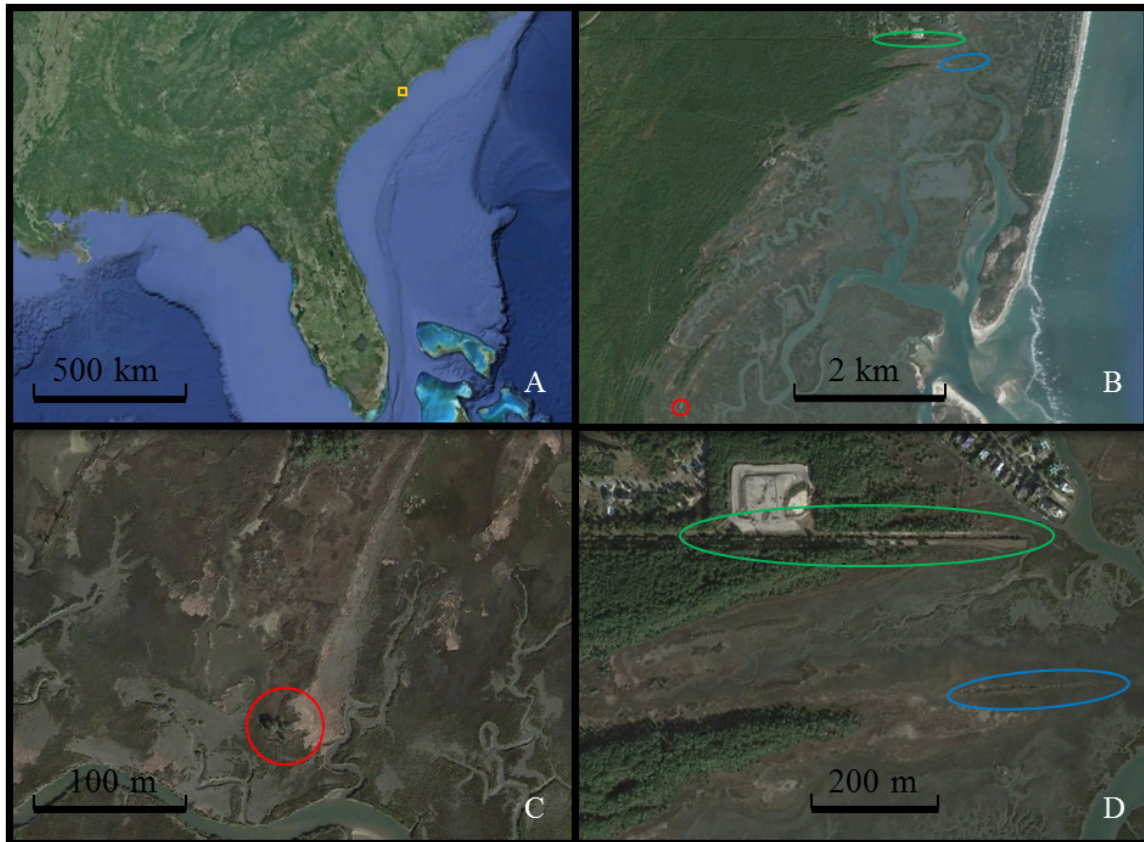


FIGURE 1. Location of study sites in North Inlet, Georgetown County, South Carolina (A-D). Study sites, island (red circle), dike (green oblong), and berm (blue oblong) were located in sandy, dry, upland habitat (B).

accessibility for efficiency of equipment transport and monitoring.

The first site was located on a near-shore island (hereafter referred to as island site) approximately $40\text{ m} \times 45\text{ m}$ in size and surrounded by high Salt Marsh (dominated by Pickleweed (*Salicornia virginica*) and Needlegrass (*Juncus roemerianus*). High Salt Marsh elevations are above mean high water levels (i.e., flooded only during higher than average high tides or storms), whereas low Salt Marsh elevations lie between mean sea level and mean high tide and are typically dominated by *Spartina alterniflora* (Adam 1993). The second site (hereafter referred to as dike site) was a raised linear embankment (approximately $5\text{ m W} \times 1.5\text{ m H} \times 400\text{ m L}$) with access to nearby low Salt Marsh via a 2-3 m wide man-made canal. The third site was a linear berm (hereafter referred to as berm site); approximately $2\text{ m W} \times 0.5\text{ m H} \times 200\text{ m L}$, surrounded by high Salt Marsh. The island and berm were both heavily vegetated by salt-tolerant vegetation while the dike site was covered by patchy grasses and salt-tolerant vegetation. All three sites had a sandy substrate. Residential developments were located within 100 m of the dike site.

Nesting activity and documentation of nest predators.—We searched the three study sites for evidence of terrapin nesting by walking transects every 2-3 d (0600–2000) from 9 May to 30 July 2013. We conducted surveys 33 d out of the approximately 65-d nesting season during both high and low tide. The berm and dike sites were monitored all survey days, while the island site was surveyed 31 of 33 d. The island site was a roughly circular area physically divided by a downed tree. We walked the perimeter and a smaller circular path within the perimeter on both halves of the island each survey day. We walked two linear transects along each edge of both dike and berm sites during each survey. During surveys, we searched the ground for terrapin tracks, evidence of nesting activity, scat and tracks from predators, eggshells, and depredated nests. For each depredated nest, we recorded the number of eggshells, condition of shells (e.g., dry, wet, presence of fresh egg contents), evidence of predators (e.g., scat/tracks), and latitude and longitude of the nest site ($< 3\text{ m}$ horizontal accuracy; Rino 650®, Garmin, Schaffhausen, Switzerland).

We also passively monitored nesting sites for nesting females and for presence of nest predators using motion-

activated cameras (Moultrie® Game Spy® M-880 Mini 8.0 Megapixel Digital Game Camera, Moultrie Feeders, Alabama, USA). We mounted cameras approximately 0.5 m above the ground on trees or existing fence posts. Two to three cameras monitored each site. We placed track boards in active animal movement corridors in areas adjacent to nesting sites and used tracks to identify potential predators. We constructed track boards using plywood sheets (approximately 61 cm W × 6 mm H × 122 cm L) coated with wet intertidal mud and smoothed with a trowel. Track boards recorded footprints over one night (10 h) following initial deployment. The day after deployment, we photographed tracks for identification. Details of imprinted tracks were sufficient to identify animals as small as rodents.

Simulated nest experiments.—We conducted three separate experiments during terrapin nesting season (approximately 24 May to 28 July 2013) using simulated terrapin nests and a series of treatments to determine the sensory cues used by predators to locate terrapin nests. Because rainfall may mask evidence of nesting turtles (Bowen and Janzen 2005; Strickland et al. 2010), we conducted all experiments during dry weather conditions. The first experiment ran from 29 May to 1 June 2013 and tested the hypotheses that Raccoons use the scent of female Diamond-backed Terrapins to locate recently constructed nests and that rain dilutes chemical cues associated with terrapin nests, thus reducing ability of predators to locate them. We constructed 40 simulated nests at each of the three study sites using a soil coring auger that extracted uniform cylinders 6 cm w × 10–12 cm in depth (natural nests in North Inlet are typically 3–4 cm diameter at the surface and 5–8 cm in the nest chamber with a mean depth of 11 cm; Scott Parker, pers. obs.). We allocated simulated nests to three scent treatments: terrapin scent ($n = 39$), neutral scent ($n = 39$), and no-scent control ($n = 42$). We obtained native fill sand from each site and we applied scent treatments within 30 min of excavating simulated nests. We created terrapin scent by placing an adult female terrapin in a 38 L plastic container (half filled with damp native sand moistened with dechlorinated tap water) for approximately 1 h (Marchand et al. 2002).

Females that we used to inoculate fill sand with terrapin scent were not gravid. Nesting female terrapins, however, frequently urinate during oviposition, thus producing a potential chemical cue identifiable by nest predators (Ernst et al. 1994; Marchand et al. 2002). Similarly, captured female terrapins voided their bladders while in the sand-filled container thus inoculating fill sand with scent (Marchand et al. 2002; Burke et al. 2005). The neutral scent treatment consisted of 2 ml CVS Pharmacy-brand aftershave liquid per 1 L of de-

chlorinated tap water (Whelan et al. 1994). We chose artificially scented water as the neutral scent because it presumably has no food-associated odor and would therefore reveal preferential predation on terrapin scented nests. The no-scent treatment consisted of native sand dampened with dechlorinated water and no added scent. We wore rubber boots and latex gloves while constructing nests, and gently tamped down nests by hand after filling. We did not place food rewards in simulated nests. It is unlikely that nest predators would become habituated to simulated nests without eggs (and therefore ignore them) considering the relatively short duration of our experiment, and we found no evidence of this in our experiments (see also Burke et al. 2005; Strickland 2010). Finally, we irrigated one half of all simulated nests across treatments with dechlorinated tap water to test whether rainfall masks olfactory cues. For the simulated rain treatment, we dispensed water evenly over nests by inverting a 19 L bucket with a perforated lid until a rain gauge suspended above the simulated nest registered 2 cm of water. We deemed 2 cm of water adequate because two previous nesting studies of turtles had observed reduced nest predation with rainfall > 1.27 cm (Bowen and Janzen 2005; Strickland et al. 2010).

To vary the spatial distribution of treatments, we constructed nests at 3–4 elevations at and above the high tide line (e.g., 0 m, 0.5 m, 1 m, 1.5 m). The high tide line was established as a reference point for nest construction because terrapins typically do not construct nests below the mean high tide line (Scott Parker, pers. obs.). We rotated nest treatments through elevations using an $n + 1$ system wherein treatments advanced one elevation after each placement (e.g., terrapin scent 0 m, neutral scent 0.5 m, control 1 m; terrapin 0.5 m, neutral 1 m, control 0 m, etc.). Because distribution of upland vegetation is associated with tidal height, our design controlled for the possibility that predators might simply follow a line of vegetation and preferentially exhume simulated nests at a given elevation. Additionally, we never placed adjacent nests closer than 1.5 m to one another. Because natural nest predation typically occurs within 48 h of oviposition (Burger 1977; Roosenburg 1992; Feinberg and Burke 2003; Butler et al. 2004), we monitored all experiments the day following setup and again 48–72 h after initial setup. We used fiberglass reel tapes and meter sticks to both lay out simulated nests at recorded locations and in the effort to relocate nests during the monitoring period. We considered nests depredated if predators dug more than 2 cm deep within a 6 cm radius of the nest. To minimize scent cross-contamination, we assigned each scent treatment and all associated gear to an individual research assistant for each experiment.

The second experiment (15–17 June 2013) tested the hypothesis that disinterred soil is the primary cue used

by predators to identify terrapin nests. In this experiment, we used the same three scent cues but applied them to simulated nests without overturning soil, while in a fourth treatment, we removed soil from the simulated nest and replaced as before (i.e., experiment one) but with no added scent. We created terrapin scent as before except that the female terrapin was placed in dechlorinated water only (no sand) for 1 h. Neutral and no-scent treatments used dechlorinated water only, with neutral scent added in the same ratio as described previously. To inoculate soil with scent treatments, we inserted a 3-cm diameter, thin-walled, steel pipe 11 cm into the substrate at each simulated nest site. Loose sand allowed us to push the pipes in by hand, disturbing only the relatively small amount of soil in contact with the pipe. The bottom 9 cm of pipe was perforated to allow scent-treated water (250 ml per nest) to seep into the substrate of the simulated nest. Scent treatments thus irrigated a column of sand similar in volume to that of a natural terrapin nest. Tightly fitting dowels were inserted into each pipe to hold soil cores in place (i.e., not rising above ground level) while the pipe was extracted from the ground. Using this procedure, we were able to localize scent treatments into soil cores without excavation. We constructed 14 simulated nests per treatment at each of our sites ($n = 56$ nests per site) and we rotated treatments through elevations in the same manner as experiment one.

The third experiment (16-20 July 2013) tested the hypothesis that the scent from freshly excavated soil is the olfactory cue used by Raccoons to locate terrapin nests. We excavated 28 simulated nests at each site with the auger and refilled those nests within 10 min using the recently removed soil as described previously. Immediately following construction of simulated nests, we placed Raccoon exclusion cages (ca. 18 cm diameter) over simulated nests (Buzuleciu et al. 2015). We constructed cages by laying a square of wire mesh (20×20 cm with 1 cm sq. grid) over the opening of the simulated nest. We then pushed 10-12 wooden dowels (4 mm wide \times 30 cm long; soaked in water overnight to make them pliable) vertically through the wire mesh and approximately 8-10 cm into the soil, encircling the nest and pinning the mesh to the ground. We gathered and twisted together dowel tops approximately 4 cm from the end and held them in place with a wrap of metal tie wire. The resulting exclusion cage thus resembled the top of a birdcage. We left caged nests undisturbed in the field for 48 h. Caging freshly excavated nests for 48 h presumably allowed the majority of volatile soil compounds to dissipate prior to the start of the experiment. Fifty-nine cages (70%) were successful at excluding Raccoons for 48 h, while 25 nests were excluded from the experiment following cage failure. After the 48 h

interval, we constructed 28 additional, non-caged, simulated nests per site using the auger, as previously described, and we replaced the soil core into the simulated nest within 10 min with no added scent treatment. Additionally, we marked half of all simulated nests (caged and newly constructed) with marking tape tied to the top of a dowel (20 cm length), which was inserted into the center of the nest. Marking was used to test whether Raccoons use visual cues to identify nests. Again, we rotated treatments through elevations following the $n + 1$ organization used in both earlier experiments. On the afternoon of the third day, immediately following completion of the excavated/refilled simulated nests, we removed all cages. We left all previously caged (now considered aged) and freshly excavated/refilled nests overnight. We recorded frequency of depredated simulated nests beginning the following morning.

Statistical analyses.—We used groups of logistic regression models for each simulated nest experiment to identify important sensory cues used by predators to locate Diamond-backed Terrapin nests. Groups of candidate models examined for each experiment were based on the hypotheses described above. We restricted models to main effects and two-way interactions due to sample size limitations (i.e., higher order interactions led to separation or quasi-separation of the data). We analyzed data with R statistical software (R version 3.2.2; R Core Team 2015), and we used the iteratively reweighted least squares method to fit models (glm function). For each experiment, we calculated Bayesian information criterion (BIC; Schwarz 1978), information loss (Δ BIC; Raftery 1995), and Schwarz weights (w_i ; Wagenmakers and Farrell 2004; Link and Barker 2006) for all models, then these were used to select the most likely model from each set of candidate models. Bayesian information criterion provides a method for comparing the likelihood of models fitted on common data, with increasing likeliness corresponding to lower BIC values (Raftery 1995; Murtaugh 2014). Information loss is defined as the difference in BIC values between Model i and the model with the minimum BIC value. Schwarz weight is the probability that Model i is the true model, assuming the true model is included in the suite of models examined (Link and Barker 2006). Finally, we calculated coefficient estimates, odds, and odds ratios (95% CIs) for variables contained in the most likely model for each experiment. We calculated odds ratios in relation to the rain treatment in experiment 1, excavated treatment in experiment 2, and caged treatment in experiment 3. We calculated Moran's I (Moran 1950) for each site and experiment to test for spatial autocorrelation of depredated nests (R version 3.0.3; R Core Team 2014). We used an alpha level of 0.05 for tests of spatial autocorrelation.

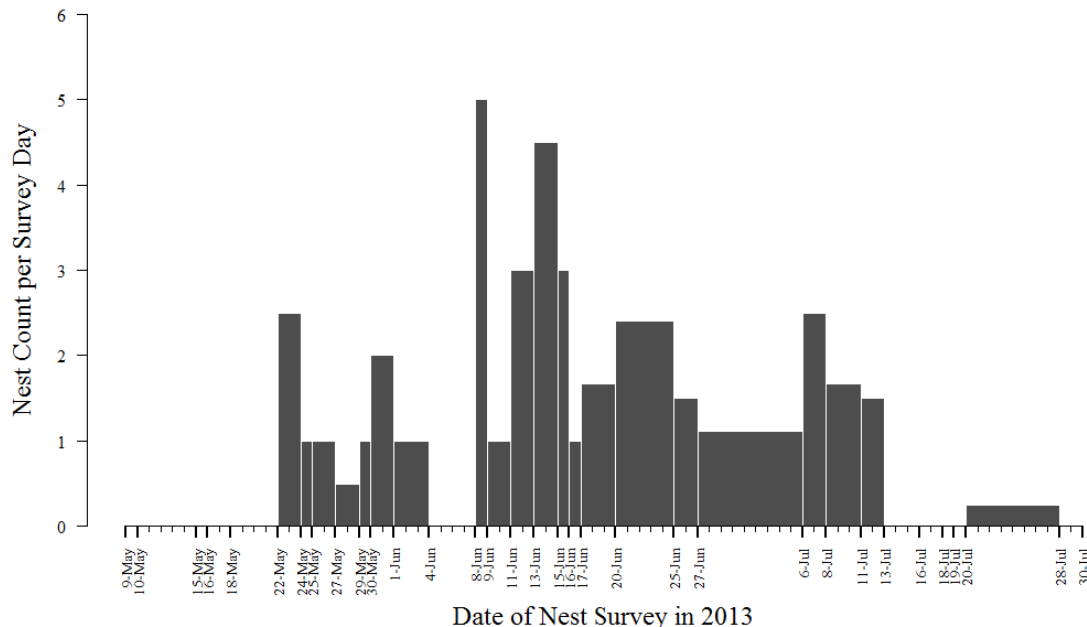


FIGURE 2. Mean daily predation per bin of nests of Diamond-backed Terrapins (*Malaclemys terrapin*) from 09 May to 30 June 2013 ($n = 89$). X-axis represents survey days. Twelve survey days with no new depredated nests are included as indicated by bin values of zero. Bin width represents days between surveys while date to the right of each bar denotes date of completion for that survey period.

RESULTS

Nesting activity.—We identified 89 depredated natural terrapin nests, identified by excavated nest chambers and eggshells scattered near the opening of the nest. All eggs within a nest were consumed and no intact eggs remained; we found no intact nests. We found four nests on the island site, while the dike and berm had 36 and 49 nests, respectively. We observed the first nests 24 May and nesting increased during June, peaking around 9 June (Fig. 2), with a maximum of five nests recorded on any day. Frequency of depredated nests declined during July and we did not observe any new nests after 28 July. The eight-day interval ending on 28 July yielded the fewest nests per day (two nests; 0.25 nests/d).

During 165 h of searching, we did not directly observe any gravid female terrapins engaged in nest construction. One lethargic female terrapin was observed under vegetation at approximately midday, at the berm site. After 30 min of observation, we captured her by hand and determined that she was not gravid (assessed by palpation). A thorough search of the area failed to produce evidence of any new nest construction. We observed a second female during nest construction by motion-activated camera.

Nest predators.—Using scat, tracks, photographs and direct observation, we recorded six potential predators within our study sites: Raccoon; Bobcat (*Lynx rufus*); Feral Hog (*Sus scrofa*); Red Fox (*Vulpes vulpes*); Black Bear (*Ursus americanus*); and one unidentified rodent.

Bear scat was the only evidence of a Black Bear near our sites and we observed the scat just prior to the start of nesting season. We saw no evidence of rodents depredating nests within our sites. Camera traps captured 461 images of animals visiting our three sites, including four of the six potential predators: Raccoon ($n = 182$); Bobcat ($n = 4$); Feral Hog ($n = 1$); and Red Fox ($n = 1$). Female terrapins were identified in four images but only depredated nests were found near the image locations in subsequent surveys.

Raccoons depredated 87 of 89 natural nests identified in our visual surveys. Raccoons typically dig neatly into the neck of the nest chamber and pile soil at the mouth of the nest making it relatively easy to identify nests excavated due to Raccoon predation. Unknown predators excavated the remaining two nests. These nests had soil strewn over a large area and pushed aside in several low mounds. We found a badly degraded paw print (either a feline or large canine track) near these nests. Moreover, two Bobcats and one Red Fox were also photographed at this site (dike site) during nesting season.

Simulated nest experiments.—Overall, 231 of 431 simulated nests were disinterred during the three experiments. Based on tracks, scat, and photographs, Raccoons likely made all 231 excavations. No evidence of predation by any other type of predator was observed during the experimental monitoring periods. Calculation of Moran's I showed no spatial clustering of depredated nests at any site, during any of the three experiments (values listed in order, from experiments

TABLE 1. List of competing logistic regression models that were used to test hypotheses about factors affecting Diamond-backed Terrapin (*Malaclemys terrapin*) nest predation in three different experiments. Bayesian information criterion (BIC) values were used to rank the candidate models. Δ BIC equals the difference in BIC values between Model *i* and the model with the minimum BIC value. Schwarz weight (w_i) is defined as the probability that Model *i* is the true model, assuming that the true model is included in the suite of models examined. The lowest BIC value and greatest w_i corresponded to the most likely model. All models with interactions also included terms for the main effects of each variable.

Model	n parameters	BIC	Δ BIC	w_i
<i>Experiment 1</i>				
Moisture	2	146.65	0.00	0.490
Location	3	147.35	0.71	0.344
Elevation	3	150.15	3.50	0.085
Scent	3	150.39	3.75	0.075
Scent + location	5	155.80	9.16	0.005
Scent + elevation	5	158.72	12.08	0.001
Scent x moisture	6	164.51	17.87	< 0.001
Scent x location	9	167.48	20.84	< 0.001
Scent x elevation	9	176.95	30.31	< 0.001
<i>Experiment 2</i>				
Excavation_scent	4	199.45	0.00	0.949
Excavation_scent + location	6	205.46	6.01	0.047
Excavation_scent + elevation	7	210.36	10.91	0.004
Excavation_scent × location	12	227.94	28.49	< 0.001
Location	3	233.46	34.01	< 0.001
Excavation_scent × elevation	16	236.23	36.78	< 0.001
Elevation	4	239.17	39.72	< 0.001
<i>Experiment 3</i>				
Cage + marking	3	132.29	0.00	0.480
Cage	2	132.71	0.42	0.389
Cage + location	4	135.91	3.62	0.079
Cage × marking	4	136.89	4.59	0.048
Cage + elevation	5	143.17	10.87	0.002
Cage × location	6	143.84	11.54	0.001
Cage × elevation	8	156.98	24.69	< 0.001
Location	3	203.25	70.96	< 0.001
Marking	2	203.60	71.31	< 0.001
Elevation	4	215.72	83.42	< 0.001

1-3, dike site: $I = -0.041, -0.016, -0.031$ and $P = 0.678, 0.361, 0.725$; berm site: $I = -0.064, -0.010, -0.063$ and $P = 0.384, 0.447, 0.226$; island site: $I = -0.071, -0.028, -0.079$ and $P = 0.352, 0.812, 0.125$).

Experiment 1, scent treatments: Simulated-nest predation by Raccoons was not associated with scent, simulated rain, elevation, or location of treatments. Of the nine logistic regression models we examined, there was evidence supporting two models: the model containing terms for simulated rain and dry treatments ($w_i = 0.490$; Table 1) and the model containing terms for the location of the experiment ($w_i = 0.344$; Table 1). However, BIC and associated metrics only evaluate the likelihood

of a model and do not provide an indication of model performance. In this experiment, the null and residual deviances for the most likely model (dry and simulated rain model) were negligibly different (null deviance = 137.11, residual deviance = 137.07), indicating that this model was no better than a model containing only an intercept. Additionally, the 95% CI for the odds ratio of predation on a nest receiving simulated rain versus a dry nest overlapped 1.0 (95% CI = 0.48-2.49); Table 2). Therefore, we concluded that simulated rain did not affect the predation probability of simulated nests, and variables from models with higher BIC values were even less likely to affect predation. Average nest preda-

TABLE 2. Parameter estimates, odds, and odds ratios for logistic regression models that were used to test hypotheses about factors affecting Diamond-backed Terrapin (*Malaclemys terrapin*) nest predation in three different experiments. Estimates are presented for the most likely model from a suite of models that were evaluated for each experiment. Estimates are provided for two models for experiment three because there was substantial evidence for both models. Odds ratios are in relation to the first treatment listed for each experiment. The abbreviation NA = not applicable.

Treatment	Coefficient estimate (95% CI)	Odds (95% CI)	Odds ratio (95% CI)
<i>Experiment 1</i>			
Dry	1.0116 (0.4609-1.6137)	2.75 (1.59-5.02)	NA
Rain	1.0986 (0.5384-1.7162)	3.00 (1.71-5.56)	1.09 (0.48-2.49)
<i>Experiment 2</i>			
Excavated	1.2993 (0.6054-2.0981)	3.67 (1.83-8.15)	NA
No-scent control	-1.0361 (-1.7693-0.3789)	0.35 (0.17-0.68)	0.10 (0.03-0.26)
Neural scent	-1.4469 (-2.2900-0.7281)	0.24 (0.10-0.50)	0.06 (0.02-0.18)
Terrapin scent	-1.1632 (-1.9260-0.4895)	0.31 (0.15-0.61)	0.09 (0.03-0.23)
<i>Experiment 3</i>			
<i>Model 1</i>			
Fresh and unmarked	2.3717 (1.5358-3.3980)	10.72 (4.65-29.90)	NA
Fresh and marked	1.2416 (0.5942-1.9616)	3.46 (1.81-7.11)	0.33 (0.11-0.84)
Caged and unmarked	-1.2686 (-2.1111-0.5260)	0.28 (0.12-0.59)	0.03 (0.01-0.07)
Caged and marked	-2.3987 (-3.5156-1.4781)	0.09 (0.03-0.23)	0.01 (0.00-0.06)
<i>Model 2</i>			
Fresh	1.6977 (1.1421-2.3346)	5.46 (3.13-10.33)	NA
Caged	-1.7148 (-2.4923-1.0555)	0.18 (0.08-0.35)	0.03 (0.01-0.08)

tion frequency (\pm SE) across treatments for rain-treated simulated nests was $75 \pm 1.6\%$ compared to $73.3 \pm 4.1\%$ in dry scent treatments (Fig. 3A).

Experiment II, scent versus freshly excavated soil treatments: The model including terms for excavation/scent was the most likely of the seven candidate models ($w_i = 0.949$; Table 1). Addition of terms for study site, location, and elevation of nest above mean high tide line did not improve the model, and models containing only terms for elevation and location had low probabilities ($w_i < 0.001$; Table 1). The odds of predation on freshly excavated simulated nests were about 10-17 times greater than those of non-excavated, scent-treated simulated nests (Table 2). Overall predation frequencies of terrapin, neutral, and no-scent control treatments were 19%, 23%, and 26% (respectively), compared to 88% in the freshly excavated treatment (Fig. 3B).

Experiment III, flagged versus unmarked simulated nests and freshly excavated versus aged excavation treatments: The model including terms for caged/uncaged and presence of a visual cue (marking) was the most likely of the 10 candidate models ($w_i = 0.480$; Table 1). There was also evidence supporting the model only including terms for caged/uncaged treatments ($w_i = 0.389$; Table 1). Although model results indicate some avoidance of marking by Raccoons, the model only in-

cluding terms for visual cue treatments had a low probability of being the most likely model ($w_i < 0.001$; Table 1), and freshly excavated nests had a much greater odds of being depredated compared to caged nests, regardless if marking was present or not. Thus, we concluded that not caging or caging simulated nests was the main factor driving predation. The odds of predation on freshly excavated, uncaged simulated nests were about 30 times greater than that of simulated nests protected for 48 h with predator exclusion cages (Table 2). Freshly excavated simulated nests had predation rates approximately six times (85%) those of caged simulated nests (14%; Fig. 3C).

DISCUSSION

Nesting activity.—Incidence of Diamond-backed Terrapin nest predation at North Inlet had a distinct beginning (24 May), an ending on 28 July, with peak predation activity during the first half of June. Although we searched carefully for nesting females, we found only a single female engaged in nest construction (image captured using camera trap). The physical and vegetation characteristics of nesting areas in North Inlet may contribute to the difficulty locating nesting females. For example, nesting habitats in North Inlet are discontinu-

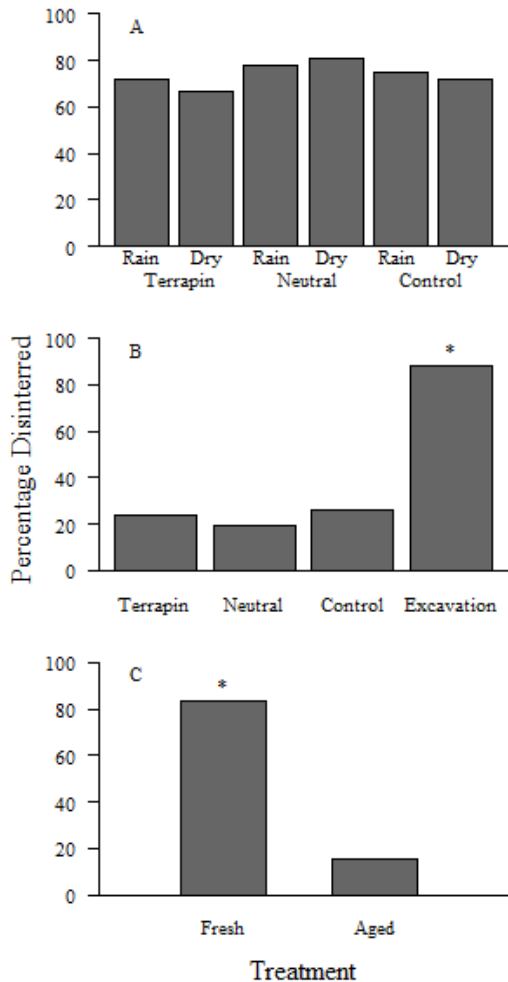


FIGURE 3. Percentage predation averaged across sites of simulated Diamond-backed Terrapin (*Malaclemys terrapin*) nests treated with experimental scent, excavation, or aging treatments: A) Frequency of predation on simulated nests treated with terrapin scent, neutral scent and no-scent control (half of each nests per treatment received simulated rain); B) Frequency of predation on non-excavated simulated terrapin nests treated with either terrapin scent, neutral scent and no-scent control versus freshly excavated simulated nests with no added scent treatment; C) Frequency of predation on freshly excavated/refilled simulated nests compared to aged simulated nests (protected for 48 h with predator exclusion cages before start of experiment; marked and unmarked treatments pooled because of minimal effect of marking-treatment on predation frequency).

ous (often separated by hundreds of meters), and tend to be covered by relatively dense growth of low halophytic vegetation such as Needlerush, Sea Oxeye Daisy (*Borrichia frutescens*), Eastern Prickly Pear Cactus (*Opuntia humifusa*), and Spanish Bayonet (*Yucca aloifolia*) as opposed to open sandy areas described in previous studies (e.g., Burger 1977; Auger and Giovannone 1979; Roosenburg 1992; Munscher et al. 2012). In absence of large, open, sandy nesting areas in North Inlet, tracking

nesting females via crawls was not possible (Butler et al. 2004). Because we were unable to locate intact, natural terrapin nests, we do not know how many natural nests with eggs survive to hatching, or what characteristics (e.g., location, timing of oviposition) might contribute to successful egg survival.

Nest predators.—Because the Diamond-backed Terrapin has a large latitudinal range, nest predators vary with population locality (Burger 1977; Ernst et al. 1994). Throughout their range, however, Raccoons are implicated as the principal nest predator in the majority of studies (Burger 1977; Feinberg and Burke 2003; Butler et al. 2004; Munscher et al. 2012). Our results support this general conclusion: out of 324 depredated nests (both natural and simulated), Raccoons were likely responsible for predation events in all but two instances. In addition to Raccoons, Red Foxes and Bobcats were identified at terrapin nesting areas and therefore could also prey upon terrapin nests. Feral Pigs were common in the study area but we do not have conclusive evidence that they specifically sought out terrapin eggs for consumption. Observations of our study sites, however, indicate feral pigs can damage relatively large areas of nesting habitat. For example, shortly after conclusion of this study, areas of the berm site were destroyed by rooting activity of feral pigs. This damage resulted in widespread uprooting of vegetation as well as a reduction in overall elevation of the nesting area (Samuel Buzuleciu, pers. obs.). The reduction in vertical height of the nesting berm made the damaged area vulnerable to tidal inundation.

Simulated nest experiments.—Our initial hypothesis that Raccoons locate terrapin nests using olfactory cues associated with female terrapins was not supported. Simulated nests in the first experiment were depredated with nearly equal frequency independent of scent treatment (terrapin scent: 69%, neutral scent: 79%, no-scent control: 74%). Our methodology used in this first experiment was similar to Burke et al. (2005); however, results of Burke et al. (2005) showed no difference in predation of no-scent vs. terrapin scented simulated nests in 2003 but a difference between the two treatments the following year (2004). While our rain treatment had the potential to provide predators a new nest location cue (i.e., a damp nest in an otherwise dry area), the rain treatment did not increase odds of nest depredation compared to dry nests. Our results differed from two previous studies that documented decreased predation rates on turtle nests when rainfall exceeded 1.27 cm/day (Bowen and Janzen 2005; Strickland et al. 2010). Because our rain treatment was limited in spatial and temporal scale it does not mimic large scale effects that would occur during storms where precipitation covers a wide geographic

area. Rainfall would also likely make physical evidence of soil disturbance caused by nest construction more difficult to detect. Under natural conditions, rainfall may also depress predator activity thus reducing foraging activity during rainy weather; if so, this may explain why the simulated rainfall treatment did not result in lower predation rates in this study. Nonetheless, our results indicate that while Raccoons likely use olfaction to locate terrapin nests, scent of the female terrapin is apparently not a primary olfactory cue.

Informed by results of our first experiment, where all scent treatments experienced high rates of predation, our second experiment supported the hypothesis that excavated soil is the primary cue used by raccoons to locate terrapin nests. There were approximately three to four times the numbers of disinterred simulated nests in the excavated nest treatment compared to non-excavated terrapin, neutral and no-scent treatments. While Burke et al. (2005) and Strickland et al. (2010) suspected surface soil disturbance as an important cue for predators foraging for turtle eggs, our experimental design allowed us to isolate sub-surface soil disturbance (i.e., excavation and not simply surface disturbance) as the cue used by raccoons foraging for terrapin nests in North Inlet. The proximate sensory cue, however, could be olfactory, visual, tactile, or combination of all three.

Our third hypothesis, that Raccoons use scent of freshly excavated soil to locate terrapin nests, also was supported. Freshly constructed simulated nests were excavated at rates over five times those observed in simulated nests covered by exclusion cages for 48 h. Caged nests presumably allowed the majority of volatile chemical compounds to diffuse out of the soil and therefore these simulated nests were less easily detected by foraging Raccoons after the exclusion devices were removed. Additionally, placement of visual markers into simulated nests across treatments allowed us to determine whether Raccoons also use visual cues to locate nests. Raccoons showed no preference for excavating simulated nests identified by visual markers. These observations are similar to previous studies conducted on mammalian predators of turtle nests in which marking nests did not have an effect on predation frequency (Tuberville and Burke 1994; Burke et al. 2005; Strickland et al. 2010). The fact that freshly constructed simulated nests experienced over five times the predation rates when compared to previously caged nests, coupled with the lack of significant effect of visual markers on frequency of nest predation, suggests that scent associated with recently excavated soil is the primary olfactory cue used by Raccoons to locate terrapin nests. One potentially confounding factor affecting our conclusions is the requisite coupling of soil volatiles with soil disturbance via the construction of our simulated nests. A fourth worthwhile experiment could determine the soil volatiles released by disturbing soil and then artificially

increase concentrations of those compounds and monitor predator activity. Separating the variables of soil volatiles and soil disturbance would be difficult, but worthwhile work. The aging effect in this third experiment allowed us to distinguish effects of disturbance and volatiles from one another temporally, as we assumed most soil volatiles dissipated after 48 h.

Soils are rich in microorganisms including bacteria, protists, and fungi (Adam 1993; Perillo et al. 2009). These microorganisms produce a variety of volatile organic and inorganic compounds via metabolism that are readily released into the air, particularly when soil is disturbed (Adam 1993; Perillo et al. 2009; Gribsholt et al. 2003). Common soil-borne compounds produced via metabolism of salt marsh soil microbes include a variety of sulfurous molecules (e.g., hydrogen sulfide and dimethyl sulfide) as well as geosmin ($C_{12}H_{22}O$, an aromatic bicyclic alcohol; Trowitzsch et al. 1981; Steudler and Peterson 1984; Perillo et al. 2009). While sulfurous compounds are metabolites of anaerobic bacteria (likely lower in abundance in nest sites comprised of porous sand), geosmin is among a suite of aerobic compounds produced by microbes in soil types consistent with terrapin nests (Trowitzsch et al. 1981). Geosmin is a ubiquitous soil compound that is largely responsible for the smell of freshly turned earth. Humans can detect the scent of geosmin in concentrations of as little as five parts per billion (Smith et al. 2002), and given the highly developed olfaction of Raccoons, it is likely that they can detect geosmin at much smaller concentrations. The release of volatile soil compounds during terrapin nest construction may therefore serve as an olfactory beacon which alerts predators to nest locations. Raccoons inhabiting coastal salt marshes may be habituated to associate presence of soil-borne volatile chemicals as indicators of food because digging activities of crabs and other invertebrate prey would also likely cause release of these compounds (Johnson 1970; Gribsholt et al. 2003; Parsons et al. 2013).

The results of this study provide strong evidence that Raccoons rely primarily on olfactory cues caused by freshly excavated soil to identify locations of terrapin nests. Once nests are located, however, Raccoons may use tactile sensory information to identify the entrance of the nest then excavate the filled-in portion of the nest chamber to extract the eggs. In this study for example, the majority of nests were precisely excavated such that the original diameter of the entrance hole and depth of the simulated nests were maintained. Similarly, appearances of naturally depredated nests suggest that they are excavated in similar fashion. These observations suggest that Raccoons may detect differences in sand density (i.e., packed versus loose) and use this information to help direct their digging efforts towards the nest chamber. Indeed, detection of differences in sand density using a thin probe is one method used by research-

ers to pinpoint the location of turtle nests in the field (after Blake 1974). Likewise, Raccoons use olfaction to detect the general location of eggs of ground nesting birds, then use forepaws to identify specific position of eggs within dense vegetation (Bowman and Harris 1980). Because tactile perception is only effective inside a relatively limited area within reach of the animal, olfactory cues are likely the primary stimuli that direct Raccoons to specific nest locations.

Assuming release of volatile chemicals from freshly constructed nests occurs over a relatively short time frame (which our data seem to suggest), eggs in nests that remain undetected for the first 24-48 h may have a substantially higher probability of survival to hatching (Congdon et al. 1983, 1987; Feinberg and Burke 2003; Butler et al. 2004). Our results are consistent with those of previous work demonstrating that the majority of nest predation occurs within 24-48 h of nest construction (Congdon et al. 1983, 1987; Feinberg and Burke 2003; Butler et al. 2004). Additionally, the probability of nests remaining undetected after oviposition may depend on stochastic events such as weather conditions, which suppress predator activity, predator foraging success, or predator density (Bowen and Janzen 2005; Strickland et al. 2010), as well as factors such as nest site selection by the gravid female (Burger 1977; Roosenburg 1994). Identification of predator-specific olfactory cues released from soil during nest construction and investigations to elucidate biotic and abiotic factors influencing probability of survival of eggs in nests are both productive and much needed directions for future studies.

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